CONSTRUCTIONAL MORPHOLOGY AND PALAEOECOLOGICAL SIGNIFICANCE OF THREE LATE JURASSIC REGULAR ECHINOIDS

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ABSTRACT. General shape of test, spine and tubercle morphologies, and ambulacral pore characteristics of three regular echinoid species from the Upper Jurassic are interpreted in functional terms. Results are compared with independent sedimentological and palaeoecological analyses of the host sediments. In *Acrocidaris nobilis* the existence of a basal P3/4 isopore phyllode suggests the development of a strong sucker disc which enabled firm attachment in a high energy hardground setting. This interpretation is corroborated by tubercle characteristics indicating firmly attached but largely immotile spines, forming a 'secondary test'. Morphological interpretation of *Rhabdocidaris rhodani* suggests a low energy, possibly partly dysaerobic, firmground setting as evidenced by (1) the exclusive occurrence of slit-like C isopores and (2) oblique tubercles with a broad muscle attachment area indicating strong, motile stalking spines. Flattened general shape, lack of aboral spines and a fairly strong sucker disc enabled *Glypticus hieroglyphicus* to crawl across very irregular topography and even browse on the undersides of corals or within an open coral framework. On the other hand, the fairly massive test suggests that elevated water energy occurred at least occasionally, so that the host oligospecific dish-shaped coral association was probably positioned at shallower depths than previously thought. It is suggested that the adaptations of some Late Jurassic regular echinoids to variable niches independently accompanied and mirrored similar adaptive strategies developed in irregular echinoids, such as the evolution of respiratory flattened tube feet or adaptations towards sedimentation.

THE morphology of an animal is determined both by functional demands and phylogenetic heritage. A functional solution to a demand, such as respiration or locomotion, may be more or less perfect, and is strongly determined by the available constructional elements provided by the phylogenetic evolution of the species. In this paper we focus on the palaeoecological potential of constructional morphology in fossil regular echinoids. The examples from the Upper Jurassic demonstrate that tube feet structure, thickness and strength of corona, as well as structure and arrangement of tubercles and spines clearly vary according to the habitat of a species. A combined functional interpretation of these features allows reconstruction of the animal's life habit and gives important clues for palaeoenvironmental interpretation.

The ambulacral system of echinoids has a distinct constructional plan allowing only certain modifications. Nevertheless, tube feet of extant echinoids exhibit a great variety of structures and functions. They are involved in locomotion, adhesion, absorption, gaseous exchange, excretion, burial, feeding and chemosensory reception. The structure of these tube feet is well documented (Loven 1883; Hamann 1887; Nichols 1959a, 1959b, 1960, 1961, 1972; Smith 1978b, 1980b). Accompanying these diversifications in tube foot structure and function there is a corresponding change in the shape of ambulacral pores, through which each tube foot connects with its internal ampulla. It has been shown for modern echinoids that the morphologies of pores and tube feet are closely linked (Smith 1978a, 1980b). Consequently, the morphological analysis of the ambulacral pores, together with an analysis of the general shape of the test and the function of spines, should be extremely helpful in palaeobiological studies. Although this is generally acknowledged, only a few morphological and palaeoecological studies on fossil echinoids exist. Moreover, these studies focus almost exclusively on irregular echinoids (Hoffmann 1914; Nichols 1959c; Ernst 1970, 1972;

Kier 1974; Seilacher 1979; Smith 1978*a*, 1980*a*, 1980*b*, 1984), where the correlation of tube foot function and pore morphology is more obvious, and where other morphological characteristics, such as general shape of the corona and density patterns of spine attachment warts, help support the functional interpretation.

The purpose of this paper is to demonstrate that the environmental demands of two Late Jurassic regular echinoids, *Acrocidaris nobilis* Agassiz and *Rhabdocidaris rhodani* Cotteau, can be reconstructed successfully by the analysis of hard-part morphologies. Both species are members of well studied invertebrate associations, which, together with the character of the sediments, allow a good control of the conclusions drawn by morphological analysis of the two echinoid species. Interpretation can be further substantiated by comparison with the constructional morphology of extant regular echinoids from comparable settings. As an application we will then show that interpretation of the constructional morphology of a third Late Jurassic regular echinoid species, *Glypticus hieroglyphicus* Goldfuss, provides important clues to the interpretation of sedimentation rate, water depth and water energy, and hence helps reconstruct a palaeoenvironment which is difficult to interpret by other criteria alone.

MATERIALS AND METHODS

The three Late Jurassic echinoid species examined were: *Rhabdocidaris rhodani* Cotteau, 1878 (Rhabdocidaridae), from the siliceous sponge facies (Oxfordian) at Jabaloyas in the Celtiberian ranges of eastern Spain; *Acrocidaris nobilis* Agassiz, 1840 (Pseudodiadematidae), from Pery/La Reuchenette in the Natica/Günsberg member (Oxfordian) of north-western Switzerland; and *Glypticus hieroglyphicus* Goldfuss, 1826 (Arbaciidae), from the Liesberg member in the Rauracian of northern Switzerland and the Microsolenid Marls at Foug/Lorraine, France (Oxfordian). None of the specimens was transported: *A. nobilis* is preserved with attached spines in life position and must have been buried by a sedimentation event; *G. hieroglyphicus* is a common, regularly occurring species within a fairly uniform biostromal coral association and is commonly preserved entire; *R. rhodani* is derived from a similarly uniform sponge association. In both cases, the additional fauna is mostly not fragmented.

Judging from the *Treatise* (Durham *et al.* 1966) and the original description there are no evident differences between *Rhabdocidaris rhodani* Cotteau and the *Rhabdocidaris* species in our material. However, *Rhabdocidaris rhodani* is known only from the Bajocian, and a longevity of a single species from the Bajocian to the Oxfordian would be exceptional for a Jurassic echinoid. Comparison of our material with the original material will be performed, but is beyond the scope of this paper. Moreover, according to Mortensen (1928) some species of the genera *Rhabdocidaris* and *Polycidaris* may need taxonomic revision. Taking these restrictions into consideration, our *Rhabdocidaris* species is designated as *Rhabdocidaris rhodani* in the present paper.

After preparation and coating with gold using an Emitech K250 splutter coater, the ambulacral pore type, and structure and arrangement of spines and tubercles were determined with a scanning electron microscope (SEM).

Comparison of our Jurassic material with extant species was performed partly using published data. However, the extant *Colobocentrotus atratus* Linnaeus, 1758 (Echinometridae), appeared particularly suited for comparison, so some specimens were studied in detail for morphological comparison. Small pieces of the test and spines of this echinoid were removed and placed in a 12 per cent. solution of NaOCl for about 90 minutes in order to remove organic tissue. They were then attached to stubs, coated with gold and examined under the SEM.

Illustrated specimens with numbers prefixed by S are housed in the Palaeontological Collection of the Institute of Geology and Palaeontology, University of Stuttgart.

Definition of terms

Terminology used for anatomical details follows the *Treatise* (Durham *et al.* 1966), except for ambulacral pore terminology, which follows Smith (1978*b*).

COMPARATIVE MORPHOLOGICAL ANALYSIS OF THE REGULAR ECHINOIDS

Shape

Acrocidaris nobilis *and* Colobocentrotus atratus. The Late Jurassic and the extant species exhibit obviously similar shapes (Mortensen 1935; Zbinden 1985). The studied specimens are more-or-less circular in outline and have a flattened to slightly concave oral surface. The diameter of the tests at the ambitus is in both cases 40 mm. The body wall is extremely thick (Table 1). The coronas are low, but the ancient *Acrocidaris* is relatively higher than modern *Colobocentrotus*. Their peristome is strongly enlarged compared with the periproct. The 'gill' slits are well developed. The ambulacra are sinuated.

Rhabdocidaris rhodani. The examined specimen shows a test completely different from that of the two species above. The corona is high, spherical, and only apically and orally slightly flattened. The diameter at the ambitus, 90 mm, is large, as is the diameter of the peristome (*c*. 40 mm). The body wall is rather thin relative to the size of the test (Table 1). 'Gill' slits are not present. The ambulacra are not as strongly sinuated as in the two species above.

Glypticus hieroglyphicus. The test is flattened, particularly at the peristome, which is much larger than the periproct. The diameter at the ambitus of the examined specimen is 18 mm. The apical system is massive and found together with the test in most cases. In relation to the size of the test, the body wall is relatively thick (Table 1), so that mechanical stability was rather high. The ambulacra are not sinuated. 'Gill' slits are well developed.

Tubercles and spines

Acrocidaris nobilis. The macro- and microstructure of the tubercles reveals that this echinoid possessed two different kind of spines, which is confirmed by rare specimens with spines undoubtedly attached. On the aboral side the tubercle areole and mamelon of the primary spines are shortened, and the platform is non-crenulated. The tubercles of the ambulacra and interambulacra are very similar in size and shape (Pl. 1, fig. 2). Interambulacral and ambulacral spines from the adradial suture are strongly asymmetrical. The milled ring from the spines is shifted here to the edge of the spine which is opposite the adradial suture (Pl. 1, figs 3, 8). The spine-length is reduced and the spines look like an anvil elongated at one side. The elongated parts of these spines overlapping the ambulacral field form a kind of roof. The associated mamelons of their tubercles are very large relative to the length and diameter of the associated spine. The spines at an interradial and perradial suture exhibit no such strong unilateral elongation. Together the spines build up a mosaic-like area out of polygons with four to seven edges. These polygons form a 'secondary test' by enclosing the corona in an imperfect way. Just above the ambitus the areole of a primary in the interambulacrum becomes enlarged, which is accompanied by crenulation of the platform (Pl. 1, fig. 2) at the ambitus. Another type of spine obviously inserts at this oral type of primary. The spine of this primary is elongated (Pl. 1, fig. 7) and triangular in cross section. Longitudinally, it is asymmetrical and curved, with the tip of the spine directed downwards.

Colobocentrotus atratus. This extant echinoid shows aboral spines of the same shape as, but smaller than, those of its fossil counterpart, *Acrocidaris* (Pl. 1, figs 1, 6). The spines next to the ambulacral field are asymmetrical and also form a roof. Together these spines build up a mosaic-like area of polygons with four to seven edges, which is comparable to *Acrocidaris nobilis*, although the extant species forms a much better developed, almost perfect 'secondary test' (Pl. 2, fig. 6). Just below the ambitus the primary spines change in shape and size, becoming elongated, rounded and club-like, but more or less flattened (Pl. 1, fig. 5). At the peristome the spines are spatula-shaped and decrease

TABLE 1. Comparison of diameter, wall thickness and height of test for the studied echinoids.

	Rhabdocidaris rhodani	*Glypticus hieroglyphicus*	*Acrocidaris nobilis*
Diameter of test at ambitus	90 mm	18 mm	40 mm
Thickness of test at ambitus	*c.* 800 μm	*c.* 600 μm	*c.* 1100 μm
Height of test	50 mm	9 mm	23 mm

in diameter (Pl. 2, fig. 5). Tubercles below the ambitus change only in size, not in shape or structure. In a fossil example this would possibly be interpreted as a simple differentiation in the size of correlated spines rather than the occurrence of another morphological spine type.

Rhabdocidaris rhodani. The tubercle of a primary spine is perforated and strongly crenulated (Pl. 2, fig. 3). The notches are slightly strengthened at the side of the adoral suture. There is no differentiation in an oral and an aboral spine-type apart from the fact that the aboral tubercles are larger. The areoles of the primary tubercles are elliptical to rounded rectangular in shape and are confluent. The tubercles below the ambitus are distorted and the mamelon is shifted towards the adapical edge of the interambulacral plate. However, the area of muscle attachment is slightly broader at the adoral suture, probably indicating that the inserting muscles pulled stronger in one direction. Likewise, the oral tubercles are slightly tilted with respect to the plate surface, so that the attaching spines were adjusted at a close angle to the corona. Spines of the genus *Rhabdocidaris* are generally slender and thorny (Mortensen 1928). This corresponds with the crenulated tubercles on the test of *Rhabdocidaris rhodani*, in which the boss does not participate very much.

Glypticus hieroglyphicus. Orally the tubercles of the interambulacra are modified into irregular, elongated elevations resembling Egyptian hieroglyphics (hence its name) (Pl. 1, fig. 4). Obviously, these interambulacral elevations could not act as attachment areas for spines. However, just below the ambitus the tubercles of primary spines are well developed and the species was definitely covered by spines, although we did not find any specimen with spines attached. The mamelon is non-perforated and non-crenulated. The areole of these tubercles is small. Minute tubercles across the ambulacra are interpreted by Hess (1975) as mamillae for minute ambulacral spines.

Pore pairs and tube feet

Colobocentrotus atratus. The pore pairs of this modern echinoid were studied by Smith (1978b). On the aboral side are crowded pores of P2 isopore type in more than one row. Orally, this echinoid develops P4 isopores (breadth of the muscle attachment area: 550 μm; diameter of a pore: 100 μm; Pl. 3, fig. 2) and forms phyllodes (Pl. 3, fig. 1).

Acrocidaris nobilis. This species shows aboral small narrow ambulacral pores which stand in one row (Pl. 1, fig. 2). The pores are P2 isopores. From the ambitus to the peristome the muscle attachment area surrounding the pores increases in size and the pore pairs change to the P4 type, realizing all transitions from P2 to P3/4 isopores. In the present material P4 isopores are well preserved only directly at the peristome (diameter of the muscle attachment area: 700 μm; diameter of a pore: 330 μm; Pl. 3, fig. 4). The area at the peristome in which pore pairs are found is enlarged and phyllodes are present (Pl. 3, fig. 3). This is comparable to the occurrence of phyllodes at *Colobocentrotus*, except for the higher density of pore pairs in the latter.

Rhabdocidaris rhodani. The ambulacral pores of the studied specimen are of the same pore type over the whole ambulacral field from the periproct to the peristome. They are large, the neural canal is small and poorly defined. The muscle attachment area is poorly developed and an interporal furrow is missing. The pores adjacent to the perradial suture are rounded, whereas the pores next to the adradial suture are elongated. The space between two pores of one pore pair is greatly enlarged to 1·8 mm. The average distance between the outer margins of pore pairs is 3·6 mm (Pl. 2, fig. 2). An interporal ridge is developed. Thin section and subsequent examination with a polarizing microscope reveals that the canals of the pores passing through the test diverge (Pl. 2, fig. 1). These pores can clearly be classified as C1 isopores.

Glypticus hieroglyphicus. On the aboral side of this echinoid P2 isopore pairs (Pl. 2, fig. 4) occur in one row (Pl. 1, fig. 4). Orally this echinoid develops transitional forms from P2 isopores to P3 and P4 isopores (diameter of the muscle attachment area: 480 μm; diameter of a pore: 100 μm; Pl. 3, fig. 6). Again, an increase of pore pairs orally led to the formation of phyllodes (Pl. 3, fig. 5).

INTERPRETATION AND DISCUSSION

Functional interpretation and palaeoecology/ecology of Acrocidaris nobilis *and* Colobocentrotus atratus

Based on the similarity of general shape and spines Mortensen (1935) and Zbinden (1985) considered that *Acrocidaris* lived on surf-washed rocks or corals as does *Colobocentrotus* today (cf. Ebert 1971; Clark 1976). The transformation of the aboral spines into a 'secondary test' obviously protected the living tissues, pedicellariae and the ambulacral tube feet, and formed a free space where the tube feet could carry out their respiratory function, even when endangered by wave action. The function of the curved oral spines is suggested as to enable wedging in crevices (Hess 1975; Zbinden 1985) or 'to make the whole oral side act as a powerful sucking disc' (Mortensen 1935). The present study shows that not only the similarity of the shape of the spines, but also the partial similarity of the tubercles and particularly the type of oral and aboral tube feet of *Acrocidaris nobilis* and *Colobocentrotus atratus*, provide further evidence for a very similar life habit for both species. Particularly, the presence of phyllode-forming oral P3/4 isopores provides a strong argument for the existence of a large sucker disk, and hence for adaptation to life on hardgrounds in a high-energy setting, an interpretation which in fossil material could be drawn even if the morphology of spines were not known. However, in *Acrocidaris nobilis* the oral phyllode is not as wide and its tube feet are not as numerous as in *Colobocentrotus*. Therefore, the Jurassic species was probably not able to live in very high-energy surf. This interpretation, based on the ambulacral pore characteristics, is corroborated by the unique preservation of spines in the studied material of *Acrocidaris nobilis*. An obvious difference from *Colobocentrotus atratus* is that the marginal spines of the latter are club-like and directed downwards, in order to touch the hard substrate and hence to tighten further the lock on the substrate. *Acrocidaris nobilis* shows a differentiation of spines too, but the spines are triangular in cross section and are much more elongate so that they probably did not achieve such a tight substrate lock.

Despite this, *Acrocidaris nobilis* seems to have been better adapted to life on surf-washed substrates than is, for example, the extant *Heterocentrotus*, which has similar triangular and elongated spines, but not a complete 'secondary test'. *Heterocentrotus* lives in somewhat less exposed places, particularly on the outer reef edge, where it can attach itself in holes and cavities by means of its additional long, massive spines, thereby protecting itself against being washed away by the surf. In terms of constructional morphology, *Acrocidaris* thus could have occupied an intermediate stage between *Colobocentrotus* and *Heterocentrotus* as regards adaptation to life in an wave-agitated environment (cf. Mortensen 1935).

The *Acrocidaris nobilis* material studied is from the Günsburg/Natica member of early Late Oxfordian age exposed in the Reuchenette Quarry of northern Switzerland. Only general

descriptions of the Oxfordian coral facies of northern Switzerland exist (Pümpin 1965; Bolliger and Burri 1970; Gygi 1986), but the site was examined briefly by us for its faunal and sedimentological development. Detailed work on the Günsburg Formation of the Reuchenette Quarry is in progress (M. Takácz, pers. comm.). At exposure, the transition from the coral facies to the purely marly, more distal, slope facies of the Effingen Formation is rapid and easily seen. The reefs of the Günsburg member were thought to have been positioned on a slope break by Gygi (1986), although no morphologically sharp break is developed. The reefs are well developed and contain abundant corals in massive and bushy growth forms which, together with a large number of microbial crusts, commonly form a rigid framework. The accompanying fauna is rich and includes abundant crinoid and echinoid fragments, a diverse bivalve fauna (pectinids, limids, oysters), besides gastropods (including nerineids), terebratulid and rhynchonellid brachiopods, and a rich encrusting fauna of serpulids, bryozoans, microencrusters, etc. (Text-fig. 1). Reefs, with thicknesses of metres up to several tens of metres, arose from the sea floor. They contain frequent marl levels indicating tranquil water conditions. However, abundant debris within and at the lateral reef margins as well as marginal debris fans and upwards transition into cross-bedded calciclastic sands show that reefs were regularly affected by high energy conditions. Apart from the dense coral cover, the abundance of microbial crusts together with the rich encrusting fauna and common lithophagid borings shows the wide distribution of hard substrates as well as the lack of background sedimentation during the major episodes of reef formation. Obviously, the functional interpretation of *Acrocidaris nobilis* as adapted to hard substrates and very high energy conditions concurs perfectly with the same interpretation derived independently from the composition and structure of the host reefs.

Functional interpretation and palaeoecology of Rhabdocidaris rhodani

The inclination of the tubercles of *Rhabdocidaris rhodani* and the distortion of the mamelon to the adapical edge of the areole are obvious adaptations for supporting spines attached obliquely and adjusted at a relative close angle to the corona. The tips of the spines are directed downwards. These spines enabled *Rhabdocidaris rhodani* to stalk over the sea-floor. Stalking on slender spines is only possible if sinking into the sediment is prevented either by a generally moderately firm substrate or by a restriction of the echinoid's activity to patches of suitable substrate. Also, the areoles form a much larger portion and the boss a much smaller portion of the tubercle when compared with tubercles from *Acrocidaris* or *Colobocentrotus* in which the spines' primary function is to provide rigidity.

In Recent cidaroids it is reported that they are not able to lift themselves up when the spines are removed (Lawrence 1976a). The presence exclusively of C1 isopores indicates that its tube feet had only a respiratory function and did not help in locomotion or other activities such as particle handling or attachment. Therefore, the only means of locomotion for *Rhabdocidaris rhodani*, was

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EXPLANATION OF PLATE 1

Figs 1, 5–6. *Colobocentrotus atratus* Linnaeus, 1758. 1, aboral spine, underside, milled ring positioned marginally; note similarity to aboral spines of *Acrocidaris nobilis* (fig. 3); × 17. 5, oral spine, oblique basal termination is similar to that of *Acrocidaris nobilis*, although size and shape differs; × 8. 6, aboral spine, side view; note similarity with aboral spines of *Acrocidaris nobilis* (fig. 8); × 17.

Figs 2–3, 7–8. *Acrocidaris nobilis* Agassiz, 1840. 2, S762; top view; showing identical mamelons in ambulacras and interambulacras, ambital mamelon with large crenulated platform; note different apical tubercle shapes; × 1·4. 3, aboral spine, underside; milled ring positioned marginally; × 14. 7, tip of oral spine; × 10. 8, aboral spine, side view; milled ring positioned marginally; × 10.

Fig. 4. *Glypticus hieroglyphicus* Goldfuss, 1826; S760; top view; ambulacral pores are aligned in straight single rows; typical for the species is the complete preservation of the periproct; note lack of tubercles indicating lack of aboral spines; × 2·6.

PLATE 1
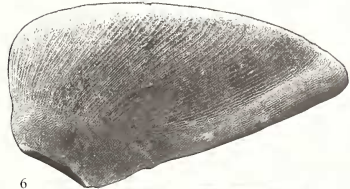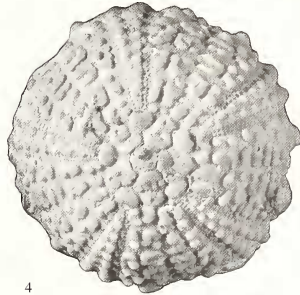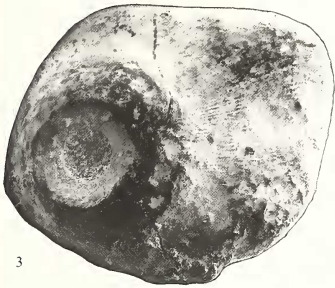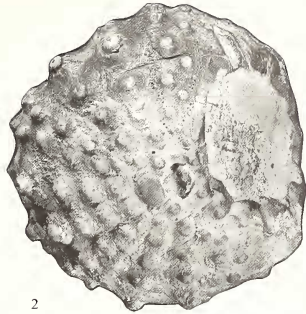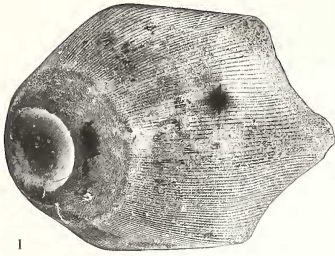
by using its spines. However, this kind of locomotion is not possible in high energy conditions, because currents might turn such echinoids upside-down due to their lack of sucker feet. In addition, the presence of well-developed C1 isopores with an exclusively respiratory function further indicates that *Rhabdocidaris rhodani* was probably adapted to life in an environment with occasional partial oxygen depletion such as a low-energy lagoon or a deeper-water setting, with impoverished water exchange, so that improvement of the respiratory apparatus was a prerequisite to thrive in such settings. Together with the obvious lack of protective spines, the occurrence exclusively of C1 isopores across the entire corona suggests that *Rhabdocidaris rhodani* could thrive only in protected caves or in environments with very low to zero sedimentation rate, for it was not able to clean sediment from its corona with its tube feet or spines; pedicellariae were the only tools available for cleaning it.

This interpretation corresponds perfectly with the data gathered from the sedimentology and the palaeoecological analysis of the accompanying fauna of the host sediment. The preserved specimen of *Rhabdocidaris rhodani* studied in detail here was found in the Oxfordian siliceous sponge meadows from the Celtiberian zone of eastern Spain. Here, reefal meadows, composed almost exclusively of densely spaced, platy hexactinosan sponges, cover an area of at least 70 000 km². They were studied in detail by Krautter (1995). He suggested that the composition of the sponge and accompanying fauna suggests likely water depths of more than 80 m, below the storm wave zone. Sponge morphologies, very reduced stratal thicknesses and the abundance of automicritic substrate indicate almost zero background sedimentation and the prevalence of firm and hard substrates. In addition, composition and morphology of the sponge species, together with the very reduced number and diversity of species of filter-feeding organisms, such as bivalves, crinoids, brachiopods or serpulids, indicate very low nutrient levels, related largely to the lack of influx of organic and inorganic terrigeneous material together with the lack of water exchange (Krautter 1995). Lack of water circulation might have caused occasional, partial oxygen depletion of bottom waters, as suggested by authigenic glauconite, *Chondrites* horizons, framboidal pyrite as well as the dominance of faunal elements with a low metabolic activity (hexactinosan sponges, brachiopods) or a facultatively anaerobic metabolism (serpulids, some bivalves; cf. Leinfelder 1993, 1994b). *Rhabdocidaris rhodani* indicates a tranquil setting with a stable substrate (no phyllodes, crawling by an adapted spine/tubercle-system), shows no obvious adaptation to background sedimentation (lack of aboral P isopores) and was adapted to lowered rates of oxygenation (dominance of C1 isopores across the entire corona) and hence is completely compatible with the above interpretation. Automicrite formation, common in the environmental setting of the studied *Rhabdocidaris rhodani*, is generally thought to be caused by microbial films and mats (Reitner 1993; Rehfeld-Kiefer 1994; Reitner *et al.* 1995) which were the probable food source for the echinoid (Text-fig. 1).

Figs 1–3. *Rhabdocidaris rhodani* Cotteau, 1878; S761; 1, cross section through an ambital C1 isopore; pores are inclined and widely spaced (arrows); bioclastic sediment (lower part of figure) infilling echinoid test; × 13. 2, C1 isopore; characteristic is the widely spaced and elongated pore pair and the lack of muscle attachment area; × 35. 3, ambital tubercles; characteristic are oval shape, large muscle attachment area, assymetrical crenulation and central perforation; × 5.

Fig. 4. *Glypticus hieroglyphicus* Goldfuss, 1826; S760; aboral P2 isopore; muscle attachment area is poorly developed in comparison with P4 isopores (Pl. 3, fig. 6); × 80.

Figs 5–6. *Colobocentrotus atratus* Linnaeus, 1758. 5, oral region; from bottom to top: club-like oral spines, flattened spatula-shaped spines; crowded and large suckered tube feet (associated with non-visible P4 isopores); and jaws; × 4. 6, top view; 'secondary test' formed by aboral spines; × 2·4.
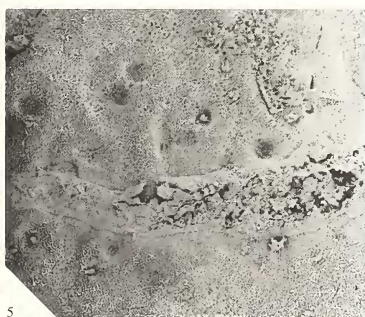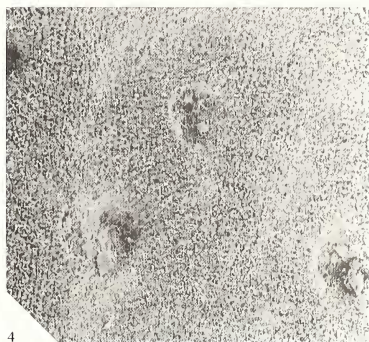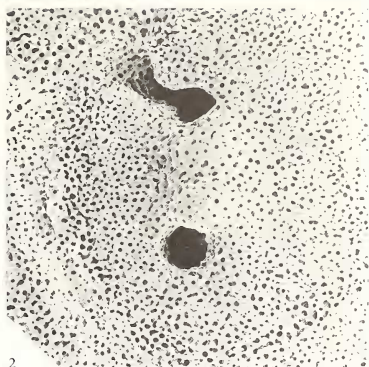
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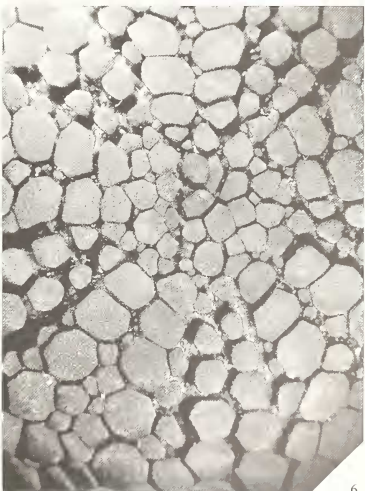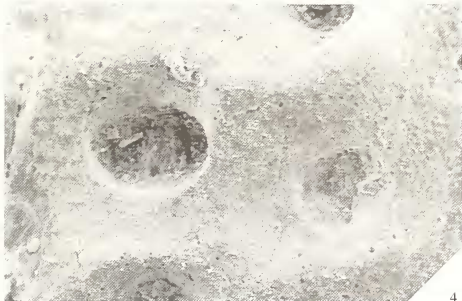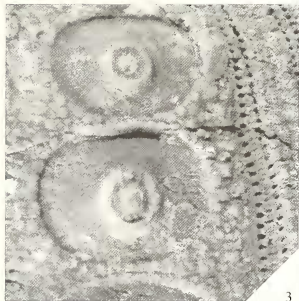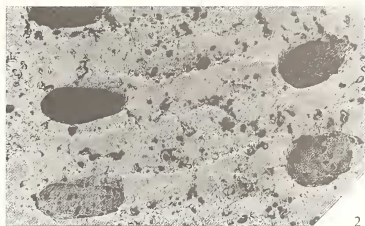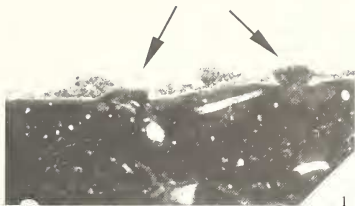
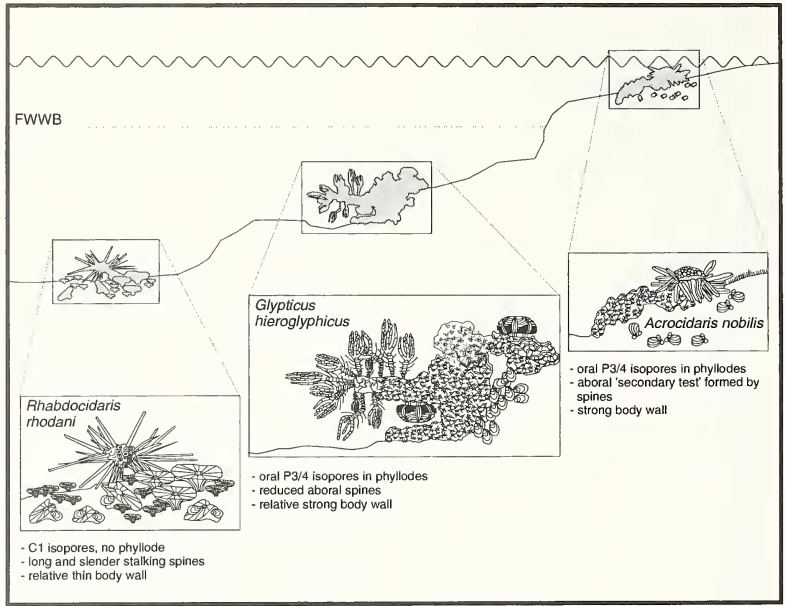*Functional interpretation and palaeoecology of* Glypticus hieroglyphicus

This echinoid shows a phylloidal tube foot configuration which appears to be functionally adapted to attach the echinoid firmly to the substrate. Very similar holdfast phyllodes exist in, for example: *Stomopneustes variolaris* (Stomechinidae), known from modern high-energy environments (Endean *et al.* 1956; Balinsky 1958; Taylor 1968, 1971); *Paracentrotus lividus* (Echinidae), from semi-sheltered areas of flat or gently sloping rock ledges (Ebling *et al.* 1960; Kitching and Ebling 1961; Neill and Larkum 1965; Gamble 1967; Crapp 1973; Allain 1975; Crapp and Willis 1975) or *Heterocentrotus mammilatus* (Echinometridae) from the outer reef edge and exposed fringing reefs in high energy environments (Tenison-Woods 1881; James and Pearse 1969; Weber 1969). The complete loss of interambulacral aboral spines in *Glypticus hieroglyphicus*, as suggested by the lack of interambulacral aboral spinal warts, cannot be interpreted unequivocally. It may point to elevated water energy, making the test flatter and smoother and hence less prone to overturning by currents or waves. In contrast, it may be interpreted also as an adaptation to an occasionally elevated sedimentation rate, for aboral spines could act as bafflers of unwanted sediment. A denuded test can be more easily cleaned of sediment, either by simple wash-off or by the activity of pedicellariae and, possibly, tube feet. Relict tiny, cilia-type aboral spines might have existed on ambulacral plates, as indicated by minute interambulacral mamillae (Hess 1975). From examination of the information available in the literature it appears that the regular echinoids with aboral suckered tube feet often cover themselves with particles to some degree. But, it seems that the covering action fulfils different functions, such as camouflage and protection from light and sediment, in different species (Lawrence 1976b). However, considering the existence of an oral sucking disk, the most likely explanation for the lack of larger aboral spines is that all mentioned features enabled *Glypticus hieroglyphicus* to move into small cavities or crawl on to the undersides of overhangs. Although the existence of spines on the oral side is obvious by the respective tubercle characteristics, no specimen with attached spines has been found. Mortensen (1935) mentioned that little is known of spines which might belong to *Glypticus*. This statement seems to be valid still today, although it might be guessed from the tubercle characteristics that *Glypticus hieroglyphicus* possessed poorly differentiated spines below the ambitus which probably helped in locomotion, although their musculature was not very strong and locomotion as well as the holdfast function must have been maintained largely by the tube feet of the oral P3/4 isopore phyllode.

The studied material of *Glypticus hieroglyphicus* is derived from the Liesberg Member of Mid Oxfordian age from Liesberg, central Swiss Jura, and from the Microsolenid Marls of Mid Oxfordian age from Foug, Lorraine, France. Oxfordian coral localities, including Foug, were studied by Geister and Lathuiliere (1991), Insalaco (1995) and Laternser (pers. comm.). The Liesberg Member has been studied by Insalaco (1995) and Takácz (pers. comm.). Both localities were investigated by us and show astonishingly similar faunal composition, fabric and sedimentology. The faunas consist largely of corals of the genera *Microsolena*, *Dimorpharaea*, *Isastrea* and *Thamnasteria*, which occur in high abundances and form platy mushroom shapes. Microsolenid corals appear to dominate strongly the association. The corals are densely spaced next

PLATE 3

BAUMEISTER and LEINFELDER, Recent and Jurassic echinoids

TEXT-FIG. 1. Life habitats of *Acrocidaris nobilis*, *Glypticus hieroglyphicus* and *Rhabdocidaris rhodani*. Diagnostic morphological echinoid features are compatible with the general palaeoecological and sedimentological analyses of the parent association. FWWB = fair weather wave base.

to each other and, particularly on their undersides, are heavily encrusted e.g. by serpulids, bryozoans and thecideinid brachiopods or crinoids. Often, a true framework is developed (Text-fig. 1).

Microsolenid corals, particularly flat growth forms, are frequently interpreted as slightly deeper water corals (Scott 1981; Werner *et al.* 1994; Nose 1995), partly comparable to the extant deep water species *Leptoseris* (Leinfelder 1994*a*; Insalaco 1995). Consequently, the locations of the present material of *Glypticus hieroglyphicus*, i.e. the microsolenid associations from Liesberg and Foug, were interpreted by Insalaco (1995) as deeper water settings, at the lower limit of coral reef growth. However, some arguments against such interpretation exist: occasional finds of platy isastreid corals in life position show corallites on the upper and lower surface (M. Takácz, pers. comm.). The encrusting foraminifer *Lithocodium* as well as the problematical form *Bacinella*, both generally considered as characteristic shallow-water indicators (Leinfelder *et al.* 1993; Schmid and Leinfelder 1995), were recently detected at Foug (Laternser, pers. comm.). Also, the development of a rigid framework is not known from the modern *Leptoseris* deep water association (Schlichter *et al.* 1985). This might indicate that water depths of the microsolenid coral association from Foug and Liesberg were shallower than generally thought and that the flat growth shape of the corals was

either a competitive feature in order to occupy all available space or was due to poor illumination caused by frequent turbidity rather than by great water depth.

Judging from the sedimentology and palaeoecology of the coral associations as well as the morphological peculiarities of *Glypticus hieroglyphicus*, the environmental setting at Foug and Liesberg was probably characterized by a moderate water depth and moderate currents. In particular:

1. The relative thickness, the irregular reinforcement structures and the flattened shape of the test of *Glypticus hieroglyphicus* might indicate occasional wave action, but the prevalence of fine-grained matrix shows that the setting was not positioned in the constantly wave-agitated zone.

2. The occurrence of phyllodes with *Glypticus hieroglyphicus* shows that it was necessary for the animal to attach firmly to a substrate. Since consistently high water-energy can be ruled out by the criteria mentioned above, phyllodial development might be interpreted as an adaptation to browsing not only on the upper surfaces but on the undersides of coral plates too. This might be additional indirect evidence for a moderately shallow setting, because it was probably light-dependent algae on the undersides of the corals which were rasped off by the echinoid. Another theoretical functional interpretation of the phyllode, as an organ for sediment feeding similar to that in many irregular echinoids, can be ruled out by the common occurrence of P3 and P4 isopores within the phyllode, pointing to the existence of many strong P3 and P4 tube feet with pure holdfast functions and by the almost exclusive occurrence of coral hardgrounds in the environments. However, modern sediment-feeding regular echinoids are known from deep water environments (e.g. *Phormosoma placenta* Thomson). A species of the Late Jurassic regular echinoid *Pseudodiadema* exhibits phyllodes. The tube feet were probably used for transport of food particles, in the same manner as in modern *Strongylocentrotus droebachiensis* (Himmelmann and Steele 1971). *Pseudodiadema* was found by us near Foug in the Oxfordian Terrain a Chailles, France, underlying the Microsolenid Marls. The marl sediments represent softground associations composed of rhynchonellid brachiopods, epifaunal, semi-infaunal and burrowing bivalves (cf. Geister and Lathuiliere 1991) and the irregular echinoid *Collyrites*, amongst others. Transportation processes (Nebelsick 1990, 1992) can be largely ruled out by the generally unfragmented preservation (Kidwell and Baumiller 1990) of the fauna. Although the preservation of the specimen does not allow closer inspection of the phyllodial pore types, we presume that this species of *Pseudodiadema* might have been a soft-ground sediment feeder.

3. The predominance of P2 isopores on the aboral side of *Glypticus hieroglyphicus*, which indicates the presence of motile, muscle-supported tube feet with a small sucker, together with the lack of spines would have facilitated biological and physical removal of sediment particles and hence appear to be an adaptation to sediment smothering. Since aboral spines are lost, this echinoid with aboral suckered tube feet may also have covered itself with particles for protection to some degree. Such adaptations on one hand, and the general low sedimentation rate as highlighted by the high encrustation rate, shows that sedimentation was intermittent rather than continuous.

CONCLUSIONS

The nature of the substratum is the primary factor influencing the local distribution of echinoids. From echinoid larvae today it is well known that they show a strong substrate preference and can suppress settlement until a suitable substratum is found. In almost all species, a strong correlation thus exists between adult distribution and the nature of the sea floor. For regular echinoids this was demonstrated by, for example, Heatfield (1965), Ernst (1973) or Sheperd (1973). Substrate characteristics are also dependent directly upon current velocities and the extent of water turbulence, factors which also determine echinoid distribution. Life in the high energy zone demands special adaptations. The presence and intensity of the sedimentation also influences distribution of echinoids, either by directly smothering the organism or by influencing substrate characteristics. In some cases regular echinoids react more sensitively to suspension in the water than do other invertebrates, including corals (Moore et al. 1963).

The reefal settings of the Upper Jurassic comprise different reefal litho- and biofacies due to differences in water energy, water depth and sedimentation rate (Leinfelder 1993, 1994b). These are the prime factors leading to differences in substratum characteristics which explains the different echinoid faunas. As discussed above, nutrient and oxygen levels are other important factors determining the composition of Late Jurassic reefs and obviously also influenced the distribution of regular echinoids.

The present study shows that morphological elements of regular echinoids, particularly general morphology and thickness of the corona, shape, structure and spatial patterns of tubercles, mamelons and spines, as well as morphology, differentiation and spatial arrangement of ambulacral pores, are important tools in interpreting the palaeoecology of the extinct animal. However, comparison with interpretations derived independently from palaeoecological and sedimentological analyses of the host rock is a prerequisite to test the correctness of the morphological interpretation as well as to choose the most likely interpretation in cases where analysis of constructional morphology results in more than one interpretation.

The constructional interpretation of *Acrocidaris nobilis* as a moderate- to high-energy, hard-ground dweller is based particularly on the interpretation of an oral phyllode with P3/4 isopores, indicative of a moderately effective, large oral sucking disk, and on the existence of a ' secondary test' formed by distally broadened and flattened, short spines whose existence could be, at least, partially concluded from the structure of the mamillae and tubercles alone. This interpretation is in perfect accordance with the interpretation of the host reef as a shallow-water, crust-rich coral reef of moderate to elevated water-energy. Frequent marl intercalations show that the 'secondary corona' of *Acrocidaris nobilis* might not only have been an adaptation to elevated water energy, but also a shelter from occasional sedimentation.

The constructional interpretation of *Rhabdocidaris rhodani* as a quiet-water, firmground species is based on the complete lack of an oral sucking disk, and the existence of stalking spines. The existence of the latter can be concluded by the asymmetrical, tilted oral tubercles surrounded by large areoles. Lack of sedimentation is indicated by the lack of aboral P and C2 isopores which would indicate the existence of motile, gripping tube feet attaching sheltering particles or performing direct sediment removal. Occasional oxygen depletion, probably caused by a certain lack of water exchange, is indicated by the exclusive, but overall presence of C1 isopores serving as respiratory feet. Again, the analysis of the low-diversity hexactinosan sponge association and sediment starvation features of the host rock suggests exactly the same interpretation.

The constructional interpretation of *Glypticus hieroglyphicus* is equivocal. The oral sucking disk composed of P3 isopores indicates the necessity for strong substrate attachment. The presence of a fairly compact corona could be interpreted as a high-energy feature. Lack of interambulacral aboral spines might indicate either a high-energy setting or a high sedimentation regime, but may also have served to enter narrow cavities. The existence of aboral motile tube feet, as judged from P2 isopores, can be interpreted as an adaptation towards sedimentation. The analysis of the extensively developed marly microsolenid platy coral meadows and frameworks helps in interpreting the function of these features. It indicates that *Glypticus hieroglyphicus* was adapted to both hardgrounds and occasional sedimentation. The compact corona indicates adaptation to occasionally elevated water energy, hence supporting other indicators for a water depth much shallower than previously thought. However, the richness of fine sediments, together with the irregular framework of platy, superimposed corals, suggest that the strong sucking disk as well as the lack of aboral spines must be seen as an adaptation to climbing the irregular, steep to overhanging walls of the coral framework, and possibly browsing on the undersides of coral plates, rather than indicating generally high water energy. This set of features rules out an alternative interpretation of this phyllode as an organ for deposit feeding, similar to phyllodial structures of irregular echinoids, since the weakly developed oral spines do not show any adaptation to locomotion on a softground and oral isopores are much larger than those used for feeding purposes.

When examined through a combined analysis, coronal morphology, tubercle and spine characteristics, and pore characteristics and arrangements are important tools in interpreting life

habit and environmental demands of ancient regular echinoids. Such analyses may support or refine palaeoenvironmental conclusions drawn from other data sets. Obviously, Late Jurassic regular echinoids inhibited a great variety of palaeoenvironments, and in part developments paralleled those later perfected by irregular echinoids. Consequently, Late Jurassic regular echinoids not only thrived on high and moderate energy, low sedimentation firmgrounds (e.g. *Acrocidaris nobilis*), but also grew under moderate sedimentation rate (*Glypticus hieroglyphicus*), and could occupy deeper, partly oxygen-depleted settings by improving their respirational apparatus (*Rhabdocidaris rhodani*) and might even have developed sediment feeding forms on softgrounds (*Pseudodiadema* sp.).

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